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THE ZOOGEOGRAPHY OF THE HERPETOFAUNA OF THE PHILIPPINE ISLANDS, A FRINGING ARCHIPELAGO

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INTRODUCTION

Inger, in his essay on the zoogeography of the Philippine amphibia (1954, pp. 448–510), presented the first major distributional paper for any part of the herpetofauna since Taylor's essay (1928). The first part of Inger's paper is concerned with the geological history of the Philippines, and the origins and degree of endemism exhibited by the amphibian fauna. Secondly, he discusses the pathways of entry into the Philippines in terms of the location of the nearest relatives and possible time of entry into the Philippines. He notes, for example, that the present distribution of the genus *Platymantis* (replaces *Cornufer*, Zweifel, 1967) suggests two speciation centers, one in the New Guinea-Solomons region and one in the northern Philippines; but by analogy, in comparison with some other amphibians, suggests a Papuan origin and subsequent dispersal into the Philippines. Inger therefore regards these two present centers as peripheral isolated concentrations of a once more widely distributed genus (1954, pp. 494, 497). He suggests that the bulk of the amphibians entered the Philippines by 2 major routes, the Palawan or Sulu-Mindanao routes. He discusses relative time of entry of different components of the amphibian fauna primarily in terms of extent of endemism and distance from areas occupied by presumed nearest relatives. Within the Philippines, Inger recognizes only 2 somewhat doubtful zoogeographic subdivisions. In his discussion of dispersal (pp. 475–484), he notes that both dispersal by way of earlier land connections and over-water dispersal must be considered, and he also notes, in general descriptive terms, possible routes within the Philippines.

Leviton (1963) provides the most recent discussion of zoogeography of the terrestrial snake fauna of the Philippine archipelago. His discussion is primarily concerned with extraterritorial origins, time of entry and endemism, present distributions, and the taxonomic relationships of species within the Philippines. These are considered in terms of past changes in island configurations, and probable internal pathways. He states (p. 377), contrary to Inger's views relative to the dispersal of the amphibians (Inger, 1954, p. 484), that the present distribution of the snakes can, for the most part, be explained on the basis of former land connections. He recognizes 5 faunal (serpentine) subregions within the archipelago at the present time.

Both authors very ably discuss the present distribution of the faunal element with which they are concerned in terms of traditional concepts of extraterritorial origins, pathways of entry and internal dispersal as governed by probable geological changes, time of entry, and means of dispersal.

Darlington (1957, pp. 476–541) discusses the Philippine ichthyological and herpetological faunas in the more general context of distributions on fringing archipelagoes. Immigrant patterns of distribution, where the species are distributed along the migration route with dropouts occurring linearly as determined by distance and relative dispersal abilities, are, he believes, the primary patterns exhibited in fringing archipelagoes. This basic pattern is modified for older relict groups by concentration of species on distal or proximal islands within the archipelago (p. 533).

MacArthur and Wilson (1963) propose the hypothesis that the number of species on an island represents a balance between number of species reaching the island and number of species becoming extinct per unit of time. They point out that a number of interacting variables will determine the point at which these 2 curves intersect. These include distance from source of immigrants, the species pool of immigrants, area of island concerned, or some other limiting factor such as unfavorable climate. They further propose that in time secondary radiation centers should increase with distance of islands from the major source of the fauna, when corrections are made for area or other limiting variables. They also note that the number of species decreases more rapidly for large than for small islands with increasing distance from source of colonization.

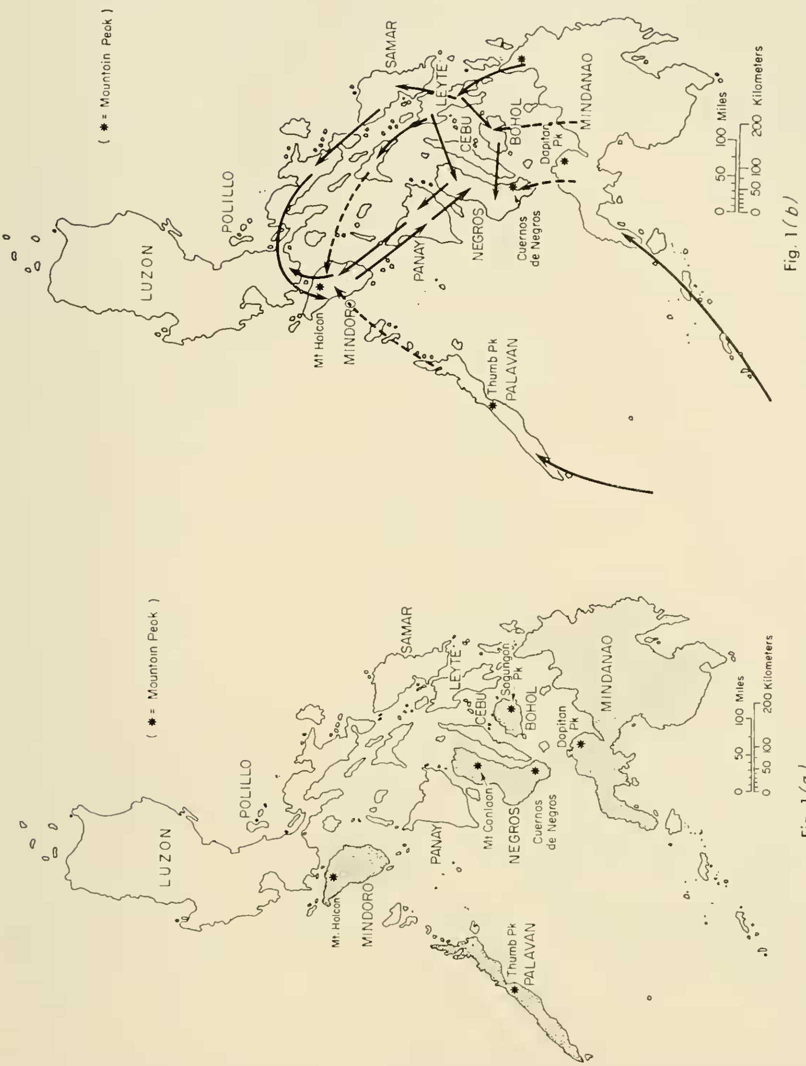

FIGURE 1. a. Islands surveyed during our recent expeditions, 1958–1963. b. Entryways and proposed dispersal routes within the Philippine Archipelago.

PROBLEMS AND METHODS

Recent intensive exploration of the herpetofaunas of 5 Philippine islands, Palawan, Mindanao, Bohol, Negros, and Mindoro (fig. 1a), makes possible more critical examination of many of the zoogeographic hypotheses suggested by previous authors. Factors which we believe make this possible are: 1) intensive sampling techniques which provide more accurate estimates of species-diversity; 2) choice of islands from proximal, distal, and intermediate regions of the archipelago (fig. 1a); 3) range in size from 5,000 to 95,000 square kilometers

Table 1. *Intensively explored areas on the five islands included in the recent survey.*

Mountain Region	*Altitude (meters)*	*Island*	*Island Area (sq. km.)*	*Exploration Date*
Cuernos de Negros	1,903	Negros (southern part)	12,700	March—May 1958 (about 7 weeks)
Mt. Canlaon	2,463	Negros (northern part)	"	March—April 1962 (about 4 weeks)
Dapitan Peak	2,199	Mindanao (Zamboanga Peninsula)	94,600	March—May 1959 (about 6 weeks)
Thumb Peak	1,286	Palawan (central part)	11,800	April—May 1961 (about 7½ weeks)
Mt. Halcon	2,580	Mindoro (northern part)	9,750	April—May 1963 (about 4 weeks)
Sagungan Mountain	870	Bohol (southeastern part)	4,100	April—May 1962 (about 4 weeks)

(table 1); 4) choice of islands which encompass sufficiently large areas of original and/or secondary lowland forest as to make negligible differences in diversity which might be due to major differences in the dominant type of plant community (see Brown and Alcala, 1964).

The techniques stressed intensive sampling of arboreal, surface, and subterranean strata in the lowland forest whenever possible, as well as selected mountains. The expeditions to each of the 6 mountain areas on the 5 islands were carried out by crews of 8 to 10 men over 4 to 7½ week periods (table 1).

Table 2. *Number of species recorded for the islands included in this study. The number in parentheses is the number of species belonging to the group of 23 widely distributed species associated with man's economy or beach communities. The number in brackets is the number of relict species.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Leyte*	*Luzon*
Caecilians	1	1					
Frogs	22 (4)[1]	34 (4)[3]	21 (3)[4]	16 (4)[4]	12 (4)[2]	16 (3)[3]	21 (4)[6]
Lizards	23 (11)[1]	52 (10)[6]	31 (11)[4]	33 (11)[4]	27 (11)[2]		34 (8)[7]
Snakes	33 (9)[0]	39 (9)[2]	20 (8)[1]	29 (9)[2]	19 (8)[1]	18 (7)[1]	39 (9)[3]
Total	78 (24)[2]	125 (23)[11]	72 (22)[9]	78 (24)[10]	58 (23)[5]		94 (21)[15]

TABLE 3. *Amphibians known from Palawan, Mindanao, Bohol, Negros, Mindoro, Leyte, and Luzon islands.*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Leyte*	*Luzon*
1. *Ichthyophis monochrous*	×	×					
2. *Barbourula busuangensis*	×						
3. *Ansonia mcgregori*		×					
4. *Ansonia mulleri*		×					
5. *Bufo biporcatus*	×						
6. *Leptobrachium hasselti*	×	×	×		×		
7. *Megrophrys monticola*	×	×	×			×	
8. *Platymantis cornutus*							×
9. *Platymantis corrugatus*		×	×	×	×	×	×
10. *Platymantis dorsalis*		×	×	×	×	×	×
11. *Platymantis guentheri*		×	×	×		×	×
12. *Platymantis hazelae*				×			×
13. *Platymantis ingeri*			×				
14. *Platymantis subterrestris*							×
15. *Micrixalus mariae*	×						
16. *Ooeidozyga diminutiva*		×					
17. *Ooeidozyga laevis*	×	×	×	×	×	×	×
18. *Rana cancrivora*	×	×	×	×	×	×	×
19. *Rana erythraea*				×			
20. *Rana everetti*		×		×		×	×
21. *Rana leytensis*		×	×	×		×	
22. *Rana limnocharis*	×	×		×	×		×
23. *Rana magna*	×	×	×	×	×	×	×
24. *Rana microdisca*	×	×					
25. *Rana nicobariensis*	×						
26. *Rana sanguinea*	×						
27. *Rana signata*	×	×	×		×	×	×
28. *Rana woodworthi*							×
29. *Staurois natator*	×	×	×			×	
30. *Philautus acutirostris*		×					
31. *Philautus bimaculatus*		×	×				
32. *Philautus leitensis*			×			×	
33. *Philautus longicrus*	×						
34. *Philautus pictus*	×						
35. *Philautus schmackeri*					×		
36. *Philautus spinosus*		×	×				
37. *Philautus williamsi*							×
38. *Rhacophorus appendiculatus*		×	×	×			
39. *Rhacophorus everetti*	×						
40. *Rhacophorus emembranatus*		×					
41. *Rhacophorus leucomystax*	×	×	×	×	×	×	×
42. *Rhacophorus lissobrachius*		×	×				
43. *Rhacophorus pardalis*		×	×	×			×
44. *Rhacophorus surdus*		×					×
45. *Pelophryne albotaeniata*	×						

Table 3. *Continued.*

	Palawan	Mindanao	Bohol	Negros	Mindoro	Leyte	Luzon
46. *Pelophryne brevipes*		×					
47. *Pelophryne lighti*		×	×				
48. *Chaperina fusca*	×	×					
49. *Kalophrynus pleurostigma*		×	×			×	
50. *Kaloula baleata*	×						×
51. *Kaloula conjuncta*		×		×	×	×	×
52. *Kaloula picta*		×		×	×	×	×
53. *Kaloula rigida*							×
54. *Oreophryne annulata*		×					

The belief that our sampling techniques for these selected mountain areas has provided a realistic estimate of the number of species present in the area is based upon experience in the Cuernos de Negros area in southern Negros Island. The initial survey expedition there in 1958, using the sampling methods noted above, resulted in the recording of 67 herpetofaunal species (Brown and Alcala, 1961, p. 631). Although extensive resampling of this area has occurred during the interim of several years, in connection with our population and other ecological studies, only 7 additional species (*Hemiphyllodactylus typus, Lepidodactylus christiani, L. lugubris, Luperosaurus cumingi, Brachymeles tridactylus, Typhlops cumingi*, and *Boiga angulata*) have been found in the southern Negros area. The 4 remaining species in the present list for Negros (tables 3, 4 and 5) are known only from the northern part of the island. Thus, even though Bohol, Palawan, and Mindoro are not yet widely explored, the presently available data on their herpetofaunal communities, based on past records and on our intensive sampling of selected mountain areas, are believed to be sufficient to realistically approximate their relative positions in terms of diversity.

Utilizing primarily the data from the 6 recently intensively explored mountain areas on 5 islands (table 1), supplemented by available lists of species, largely based on data assembled by earlier explorers, for Leyte and Luzon islands as well as total distributional data for a few genera, we propose to examine: 1) the nature of the relict patterns for some of the older herpetofaunal elements; 2) the probability of secondary radiation zones; 3) the relative importance of probable internal migration routes, using Sorenson's index of similiarity; 4) the probable importance of marine barriers in effecting the present distribution patterns; 5) the relation of island size and distance to diversity of species.

RESULTS

Diversity of Species

A total of 9,000+ herpetofaunal specimens, ranging from about 1,000 for Mindoro Island to 2,500 for Negros Island, were collected during our recent expeditions. Classification of the collected material when added to earlier records, reveals 197 species: 1 caecilian, 49 frogs, 82 lizards, and 66 snakes for these five islands (tables 2–5). Although the new records ranged from 61 for Bohol to 5 for Mindoro, only 14 were new species or species not recorded from the Philippines prior to our intensive sampling. Most of these 14 were from Palawan and Mindanao, the islands adjacent to Borneo.

The number of species of snakes and frogs recognized from Luzon and Leyte islands are based primarily upon Inger's review of the Philippine amphibia (1954) and Leviton's review of the snakes (1963). The distribution of the species of the genus *Calamaria*, however, is from Inger and Marx (1965). The list of lizards for Luzon is based primarily on the earlier records of Taylor (1922a, 1922b, 1922c, 1923 and 1925) with a few recent additions by the present authors. The inclusion of Luzon adds 23 more species (5 amphibians, 10 lizards, and 8 snakes) to the 197, making a total of 220 species (tables 3–5).

Native Fauna

Twenty-three of the 220 species (4 frogs, 11 lizards, and 8 snakes) are regarded as probably nonnative; that is, as possibly introduced or at least reintroduced by man. We do not presume that this list includes all species which have at any time been introduced by man, intentionally or otherwise. It probably, however, does include most of these species which are readily, perhaps often accidentally, transported from island to island. To be included in this category, the species must meet these criteria: 1) occur on at least 4 of the 5 islands included in our study; 2) exhibit no subspeciation except for the Palawan populations in some instances; 3) be associated with man's habitations, and cultivated lands, or with other lowland beach communities (Brown and Alcala, 1964); 4) be widespread in Borneo and other adjacent areas. It is interesting to note (table 2) that the number of species of this nonnative group, whether we are concerned with frogs, lizards, or snakes, is essentially the same for each of the 7 islands irrespective of distance from entry-point or area of island. This we interpret as further evidence supporting their classification in this category. The 23 species include:

Amphibians:
Ooeidozyga laevis
Rana cancrivora
Rana limnocharis
Rhacophorus leucomystax

Lizards:
Cosymbotus platyurus
Gehyra mutilata
Gekko gecko
Hemidactylus frenatus
Hemiphyllodactylus typus
Draco volans
Dasia smaragdina
Emoia atrocostata
Lygosoma (Leiolopisma) quadrivittatum
Mabuya multifasciata
Mabuya multicarinata

Snakes:
Typhlops braminae
Python reticulatus
Ahaetulla prasina
Dendrelaphis pictus
Chrysopelea paradisi
Elaphe erythrura
Lycodon aulicus
Psammodynastes pulverulentus

Table 4. *Lizards known from Palawan, Mindanao, Bohol, Negros, Mindoro, and Luzon islands.*

	Palawan	Mindanao	Bohol	Negros	Mindoro	Luzon
1. *Cosymbotus platyurus*	×	×	×	×	×	×
2. *Cyrtodactylus agusanensis*		×				
3. *Cyrtodactylus annulatus*		×	×			
4. *Cyrtodactylus philippinicus*				×	×	×
5. *Cyrtodactylus redimiculus*	×					
6. *Gehyra mutilata*	×	×	×	×	×	×
7. *Gekko athymus*	×					
8. *Gekko gecko*	×	×	×	×	×	×
9. *Gekko mindorensis*					×	
10. *Gekko monarchus*	×	×		×		
11. *Gekko palawanensis*	×					
12. *Hemidactylus frenatus*	×	×	×	×	×	×
13. *Hemidactylus garnoti*					×	×
14. *Hemidactylus luzonensis*						×
15. *Hemiphyllodactylus typus*	×		×	×	×	
16. *Lepidodactylus aureolineatus*		×	×			
17. *Lepidodactylus christiani*				×		
18. *Lepidodactylus herrei*				×		
19. *Lepidodactylus lugubris*				×		
20. *Lepidodactylus naujanensis*					×	
21. *Lepidodactylus planicaudus*		×	×			
22. *Luperosaurus cumingi*				×		
23. *Luperosaurus joloensis*	×					
24. *Perochirus ateles*		×				
25. *Pseudogekko compressicorpus*		×	×			×
26. *Pseudogekko brevipes*			×	×		
27. *Ptychozoon intermedia*		×				
28. *Calotes cristatellus*	×	×	×			
29. *Calotes marmoratus*				×	×	×
30. *Draco bimaculatus*		×				
31. *Draco everetti*			×			
32. *Draco mindanensis*		×				
33. *Draco ornatus*		×				×
34. *Draco quadrisi*					×	
35. *Draco rizali*		×	×			
36. *Draco volans*	×	×	×	×	×	×
37. *Gonyocephalus interruptus*					×	
38. *Gonyocephalus semperi*		×	×			
39. *Gonyocephalus sophiae*		×		×		
40. *Hydrosaurus pustulosus*		×	×	×	×	×
41. *Varanus salvator*	×	×		×	×	×
42. *Dibamus argenteus*	×	×		×		
43. *Brachymeles bonitae*					×	×
44. *Brachymeles elerae*						×
45. *Brachymeles gracilis*		×	×	×	×	×
46. *Brachymeles pathfinderi*		×				

Table 4. *Continued.*

	Palawan	Mindanao	Bohol	Negros	Mindoro	Luzon
47. *Brachymeles samarensis*						×
48. *Brachymeles schadenbergi*		×	×			×
49. *Brachymeles talinis*				×		×
50. *Brachymeles tridactylus*				×		
51. *Brachymeles wrighti*						×
52. *Brachymeles hilong*		×				
53. *Dasia griffini*	×					
54. *Dasia olivaceum*		×			×	
55. *Dasia smaragdina*	×	×	×	×	×	×
56. *Emoia atrocostata*	×	×	×	×	×	
57. *Emoia caeruleocauda*		×				
58. *Emoia ruficauda*		×				
59. *Lygosoma (Leiolopisma) auriculatum*				×	×	
60. *Lygosoma (Leiolopisma) pulchellum*		×	×	×		×
61. *Lygosoma (Leiolopisma) quadrivittatum*	×	×	×	×		
62. *Lygosoma (Leiolopisma) rabori*				×		
63. *Lygosoma (Leiolopisma) semperi*		×				
64. *Lygosoma (Leiolopisma) subvittatum*		×				
65. *Lygosoma (Leiolopisma) vulcanium*		×				
66. *Lygosoma (Leiolopisma) zamboangensis*		×				
67. *Lygosoma (Lygosoma) chalcides*	×					
68. *Lygosoma (Sphenomorphus) acutum*		×	×			
69. *Lygosoma (Sphenomorphus) arborens*				×		
70. *Lygosoma (Sphenomorphus) atrigularis*		×				
71. *Lygosoma (Sphenomorphus) coxi*		×		×		
72. *Lygosoma (Sphenomorphus) decipiens*						×
73. *Lygosoma (Sphenomorphus) diwati*		×				
74. *Lygosoma (Sphenomorphus) fasciatum*		×	×			
75. *Lygosoma (Sphenomorphus) jagori*		×	×	×	×	×
76. *Lygosoma (Sphenomorphus) luzonensis*						×
77. *Lygosoma (Sphenomorphus) mindanensis*		×	×			
78. *Lygosoma (Sphenomorphus) palawanensis*	×					
79. *Lygosoma (Sphenomorphus) steerei*		×	×	×	×	×
80. *Lygosoma (Sphenomorphus) stejnegeri*						×
81. *Lygosoma (Sphenomorphus) varigatum*		×	×			
82. *Lygosoma (Sphenomorphus) wrighti*	×					
83. *Lygosoma (Sphenomorphus) sp.*						×
84. *Mabuya bontocensis*						×
85. *Mabuya multicarinata*	×	×	×	×	×	×
86. *Mabuya multifasciata*	×	×	×	×	×	×
87. *Otosaurus cumingi*		×	×		×	×
88. *Tropidophorus grayi*				×		×
89. *Tropidophorus leucospilos*						×
90. *Tropidophorus misaminus*		×				
91. *Tropidophorus partelloi*		×				
92. *Tropidophorus sp.*		×				

Table 5. *Snakes known from Palawan, Mindanao, Bohol, Negros, Mindoro, Leyte, and Luzon islands.*

	Palawan	Mindanao	Bohol	Negros	Mindoro	Leyte	Luzon
1. *Typhlops braminae*	×	×	×	×		×	×
2. *Typhlops cumingi*				×			
3. *Typhlops canlaonensis*				×			
4. *Typhlops dendrophis*		×					
5. *Typhlops jagori*							×
6. *Typhlops longicauda*		×	×				
7. *Typhlops luzonensis*				×			×
8. *Typhlops mindanensis*		×					
9. *Typhlops ruber*					×		
10. *Typhlops ruficauda*							×
11. *Typhlops rugosa*		×					
12. *Xenopeltis unicolor*	×						
13. *Python reticulatus*	×	×	×	×	×	×	×
14. *Ahaetulla prasina*	×	×	×	×		×	×
15. *Aplopeltura boa*	×	×					
16. *Calamaria bitorques*							×
17. *Calamaria gervaisi*		×		×	×		×
18. *Calamaria lumbricoidea*		×	×			×	
19. *Calamaria palawanensis*	×						
20. *Calamaria virgulata*	×	×					
21. *Chrysopelea paradisi*	×	×		×	×	×	×
22. *Cyclocorus lineatus*		×		×	×		×
23. *Dendrelaphis caudolineatus*	×	×	×	×	×	×	×
24. *Dendrelaphis pictus*	×	×	×	×	×		×
25. *Dryophiops philippina*				×	×		×
26. *Dryocalamus tristrigatus*	×						
27. *Dryocalamus subannulatus*	×						
28. *Elaphe erythrura*	×	×	×	×	×	×	×
29. *Gonyosoma oxycephala*	×		×	×	×		×
30. *Hologerrhum philippinum*							×
31. *Hurria rynchops*	×	×		×		×	×
32. *Liopeltis philippinus*	×						
33. *Liopeltis tricolor*	×						
34. *Lycodon aulicus*	×	×	×	×	×		×
35. *Lycodon dumerili*		×					
36. *Lycodon mulleri*					×		×
37. *Lycodon subcinctus*	×						
38. *Lycodon tesselatus*							×
39. *Myersophis alpetris*							×
40. *Natrix auriculata*		×	×			×	
41. *Natrix chrysarga*	×						
42. *Natrix dendrophiops*		×	×	×	×		×
43. *Natrix lineata*		×					
44. *Natrix spilogaster*							×
45. *Oligodon ancorus*					×		×

Table 5. *Continued.*

	Palawan	Mindanao	Bohol	Negros	Mindoro	Leyte	Luzon
46. *Oligodon maculatus*		×					
47. *Oligodon modestum*		×		×			×
48. *Oligodon vertebralis*	×	×					
49. *Opisthotropis alcalai*		×					
50. *Opisthotropis typica*	×						
51. *Oxyrhabdium leporinum*				×	×		×
52. *Oxyrhabdium modestum*		×	×			×	
53. *Psammodynastes pulverulentus*	×	×	×	×		×	×
54. *Pseudorabdion ater*		×					
55. *Pseudorabdion mcnamarae*				×			×
56. *Pseudorabdion montanum*				×			
57. *Pseudorabdion oxycephalum*				×			
58. *Pseudorabdion taylori*		×					
59. *Sibynophis bivittatus*	×						
60. *Stegonotus mülleri*		×				×	
61. *Zaocys carinatus*	×						
62. *Zaocys luzonensis*				×		×	×
63. *Bioga angulata*		×	×	×		×	×
64. *Bioga cynodon*	×	×				×	×
65. *Boiga dendrophila*	×	×	×				×
66. *Boiga drapiezi*	×						
67. *Boiga philippina*							×
68. *Calliophis calligaster*				×	×		×
69. *Maticora intestinalis*	×	×	×				×
70. *Naja naja*	×	×	×		×	×	×
71. *Ophiophagus hanna*	×	×		×	×		×
72. *Trimeresurus flavomaculatus*		×	×	×	×	×	×
73. *Trimeresurus schultzei*	×						
74. *Trimeresurus wagleri*	×	×	×	×		×	×

In other sections of this paper, certain of the indices are determined, both for the total fauna and for the presumed native fauna following the exclusion of these 23 species.

Relict Patterns and Secondary Radiation Zones

As noted by Darlington (1957, p. 505) endemism at the specific and subspecific levels is high, but at the generic level very low for the Philippine herpetofauna. It is of interest to examine the distributional patterns of these endemic genera, as well as of a few other genera (the presumed earlier arrivals) which, though not limited to the Philippines, exhibit disrupted distributional patterns outside the Philippines, to determine their fit to typical relict or modified immigrant patterns as postulated by Darlington (1957, p. 484 ff.). This selection of endemic genera and those with strongly disrupted distributional patterns does

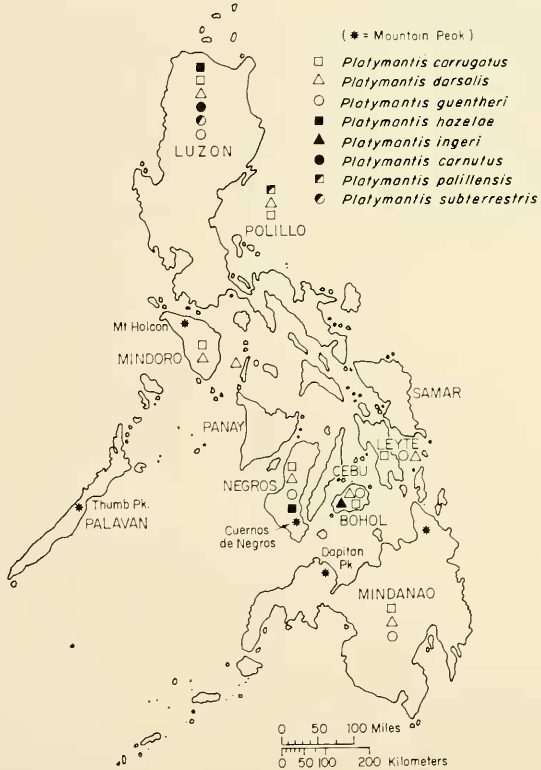

Fig 2

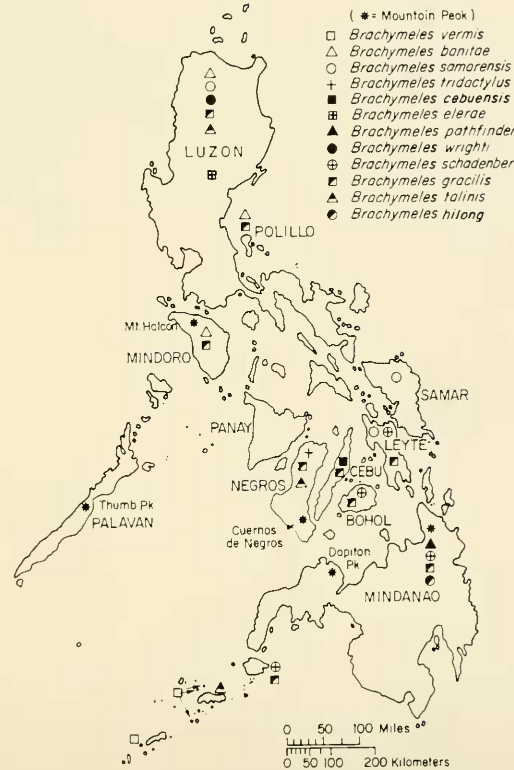

Fig. 3

FIGURE 2. Distribution patterns of species of the frog genus *Platymantis* in the Philippines.
FIGURE 3. Distribution patterns of species of the lizard genus *Brachymeles* in the Philippines.

not preclude the possibility that species in other, widely distributed genera may also be relicts of early immigrations, but provides objective criteria for selection.

The endemic genera include *Barbourula*, an amphibian; *Luperosaurus*, *Pseudogekko* and *Brachymeles*, lizards; and *Cyclocorus*, *Hologerrhum*, and *Oxyrhabdium*, snakes. *Platymantis* in the amphibia and *Perochirus* in the squamata, though not endemic, exhibit overall disrupted patterns.

Barbourula and *Perochirus* are limited to single species in the Philippines. *Barbourula* is known only from the Palawan group and *Perochirus* only from Mindanao and Leyte. This pattern of limitation to proximal islands permits 3 alternative explanations: 1) these genera have very low dispersal ability and did not go beyond these proximal islands; 2) they have reached but failed to establish themselves on more distal islands; 3) they still remain to be found on the other islands.

Platymantis, *Brachymeles*, and *Luperosaurus* exhibit relict patterns (figs. 2, 3, and 4) of the type which may be interpreted as resulting from the partial extinction of an old widespread fauna (Darlington, 1957, p. 485). Each of these genera includes several species. The genus *Platymantis* (as noted by Inger, 1954, p. 496 exhibits a concentration of species on Luzon at the distal end of the archipelago, others with distribution limited to one or two scattered islands, and several species which are widespread throughout the Philippines, though none of these species are known from outside of the archipelago. As proposed by MacArthur and Wilson (1963, p. 386) and Inger (1957, p. 496), such a pattern may also be interpreted as due in part to secondary radiation from the distal island of Luzon as indicated by the present distribution of *P. hazelae* and *P. polillensis*, very closely related species, not necessarily as wholly due to chance extinctions of once widespread species.

The genus *Brachymeles*, as reviewed by Brown and Rabor (1967), includes such widespread species as *B. gracilis* and *B. schadenbergi*, groups of species limited to the proximal or distal islands, and a third very interesting group (the tridactylus-vermis group) which strongly suggests an origin in and radiation from the center of the archipelago. Based on the presumed evolutionary relationships, indicated by the degree of reduction of the limbs and digits, the least specialized members of the group occur in the central islands and those with the greater reduction of limbs and digits in the northern and southern islands. These species include:

Species	Distribution	Digits on fore limbs	Digits on hind limbs
Brachymeles tridactylus	Negros	3	3
Brachymeles cebuensis	Cebu	3	2
Brachymeles samarensis	Leyte, Samar, and Luzon	2	2
Brachymeles bonitae	Luzon and Mindoro	0–1	0–1
Brachymeles vermis	Sulus	0	0

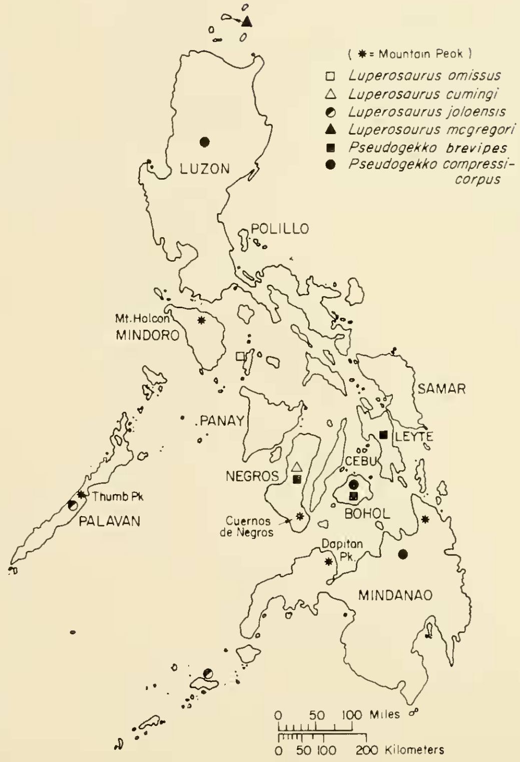

Fig. 4

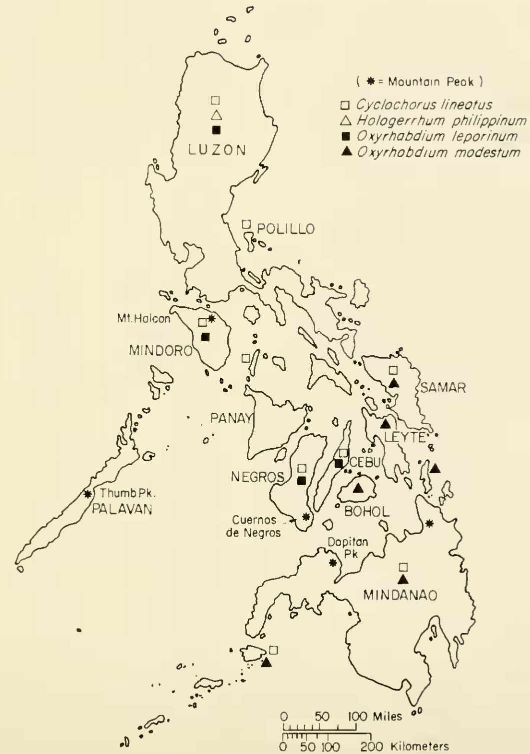

Fig. 5

FIGURE 4. Distribution patterns of the lizard genera *Luperosaurus* and *Pseudogekko* in the Philippines.

FIGURE 5. Distribution patterns of the species of the snake genera *Cyclocorus*, *Hologerrhum*, and *Oxyrhabdium* in the Philippines.

TABLE 6. *Indices of similarity for amphibians. The index in parentheses is based on the native species after exclusion of common widespread forms associated with man's economy or beach communities. The index in brackets is based on those species remaining after the relicit species are also excluded.*

	Mindanao	*Leyte*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.429 (0.333) [0.364]	0.368 (0.258) [0.296]	0.372 (0.278) [0.323]	0.263 (0.067) [0.080]	0.412 (0.231) [0.261]	0.326 (0.171) [0.214]
Mindanao		0.600 (0.588) [0.486]	0.691 (0.667) [0.634]	0.520 (0.429) [0.343]	0.476 (0.368) [0.303]	0.509 (0.426) [0.368]
Leyte			0.703 (0.645) [0.583]	0.687 (0.640) [0.556]	0.643 (0.571) [0.500]	0.595 (0.533) [0.476]
Bohol				0.541 (0.467) [0.364]	0.485 (0.385) [0.300]	0.429 (0.343) [0.240]
Negros					0.643 (0.500) [0.429]	0.703 (0.621) [0.526]
Mindoro						0.606 (0.480) [0.471]

Hologerrhum has a relict pattern exhibiting limitation to the distal island of Luzon (fig. 5). *Pseudogekko*, with two species, has a spotty distribution; *Cyclocorus* (1 species) and *Oxyrhabdium* (2 species) have less obvious relict patterns, being more widely distributed throughout the archipelago (figs. 4 and 5).

INTERNAL MIGRATION ROUTES

When differences in composition as well as diversity are considered, it is possible to compare the relative effectiveness of probable dispersal routes indicated in fig. 1b. In comparing composition of the faunas, we have used the

$$\text{similarity index } \frac{\text{twice the number of species common to the two communities}}{\text{the sum of the species comprising each of the communities}}$$

developed by Sorenson (1948) for comparing plant communities in northeast Greenland and in Denmark. A low index of similarity will be the result of either: (1) a large difference in diversity; or (2) when diversities are more or less equal, a small number of species in common.

In addition to the 5 islands upon which this study is primarily based, Leyte Island, as well as Luzon, has been included in this section since the former lies

Table 7. *Indices of similarity for lizards. (The index in parentheses is based on the species exclusive of the 23 widespread forms associated with man's economy or beach communities, that in brackets is based on the species remaining after relicit species are also excluded).*

	Mindanao	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.400	0.481	0.500	0.440	0.316
	(0.185)	(0.125)	(0.176)	(0.000)	(0.053)
	[0.213]	[0.148]	[0.207]	[0.000]	[0.067]
Mindanao		0.651	0.471	0.380	0.395
		(0.548)	(0.313)	(0.207)	(0.265)
		[0.539]	[0.333]	[0.200]	[0.218]
Bohol			0.562	0.552	0.491
			(0.333)	(0.278)	(0.348)
			[0.294]	[0.267]	[0.286]
Negros				0.600	0.478
				(0.368)	(0.333)
				[0.375]	[0.323]
Mindoro					0.590
					(0.429)
					[0.424]

closest to Mindanao on the most eastern dispersal route. The Leyte indices have been computed only for frogs and snakes, based on lists published by Inger (1954) and Leviton (1963). The lizards are not sufficiently well known to be included at this time, and the snakes are believed to be rather poorly known since several widely distributed species have not yet been reported from this island. This, however, would tend to introduce an error in the direction of a low rather than a high index.

As is evidenced in table 2, Mindanao, at the proximal end of the eastern routes, exhibits a higher diversity for each of the major taxa considered, as well as for the herpetofauna as a whole, than do any of the other 4 islands included in our expeditions. This will depress the similarity index when comparisons are made with the other islands, whereas no such depressing effect will exist in the instance of Palawan at the proximal end of the western entryway, since the diversity of the Palawan herpetofauna is about the same as that of the more distal islands which range from 60 to 80 species in total herpetofauna. Thus, if indices between Mindanao and more distal islands are equal to or greater than the indices between Palawan and these same islands, less isolation of island faunas along eastern routes from Mindanao would be indicated.

All indices, those for each of the taxa, (frogs, lizards, and snakes), as well as those for the total herpetofaunas (tables 6–9), are moderately high when

TABLE 8. *Indices of similarity for snakes. (The index in parentheses is based on species exclusive of the 23 widespread forms associated with man's economy or beach communities, that in brackets is based on the species remaining after relicit species are also excluded).*

	Mindanao	*Leyte*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.528 (0.373) [0.385]	0.431 (0.229) [0.235]	0.491 (0.278) [0.286]	0.323 (0.182) [0.190]	0.308 (0.171) [0.176]	0.308 (0.296) [0.314]
Mindanao		0.596 (0.488) [0.474]	0.644 (0.524) [0.513]	0.500 (0.360) [0.348]	0.414 (0.293) [0.268]	0.538 (0.433) [0.436]
Leyte			0.684 (0.609) [0.571]	0.468 (0.305) [0.345]	0.324 (0.182) [0.200]	0.491 (0.341) [0.378]
Bohol				0.531 (0.315) [0.345]	0.462 (0.348) [0.381]	0.542 (0.333) [0.378]
Negros					0.542 (0.516) [0.429]	0.706 (0.640) [0.622]
Mindoro						0.621 (0.585) [0.541]

Palawan and Mindanao are compared, even though the differences in diversity are relatively large. This is the result of the large number of species which these 2 entry-way islands have in common. These common species have either entered the 2 islands relatively recently from Borneo or have continued to reinvade from time to time. The fact that many of these species have not dispersed to more distal islands in the Philippines and yet are conspecific with Bornean populations tends, however, to support the first explanation of more recent entry.

When indices between Mindanao and Mindoro, Leyte, Luzon, or Negros, based on the complete fauna (both native and nonnative species), are compared with the indices between Palawan and these same islands (tables 6–9), those with Mindanao are much higher, with one exception, even though the greater diversity of the Mindanao fauna, almost twice that of Palawan, tends to depress the similarity indices. The exception is the Palawan-Mindoro index for lizards. These differences are more pronounced and the exception ceases to exist when the 23 widespread, nonnative species (p. 111) are excluded. The differences are not quite as great, in most instances, when those classified as older relicts (p. 117) are also excluded; but these latter, small differences can be accounted for by the absence of the relict genera *Platymantis* and *Brachymeles* from Palawan.

TABLE 9. *Indices of similarity for the total herpetofauna. (The index in parentheses is based on species exclusive of the 23 widespread forms associated with man's economy or beach communities, that in brackets is based on the species remaining after relicit species are also excluded).*

	Mindanao	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Palawan	0.453 (0.304) [0.331]	0.453 (0.245) [0.274]	0.372 (0.109) [0.122]	0.382 (0.165) [0.188]	0.372 (0.186) [0.214]
Mindanao		0.660 (0.584) [0.567]	0.493 (0.354) [0.337]	0.415 (0.286) [0.258]	0.475 (0.362) [0.331]
Bohol			0.547 (0.377) [0.345]	0.508 (0.364) [0.342]	0.494 (0.368) [0.337]
Negros				0.588 (0.457) [0.415]	0.616 (0.511) [0.481]
Mindoro					0.605 (0.523) [0.505]

This indicates that the primary dispersal routes for the native fauna were by way of Mindanao, and that the present herpetofauna of Palawan has not dispersed widely into other areas in the Philippines.

The high indices between Mindanao, Leyte, and Bohol are due to the very large number of species which they hold in common, even though diversity is greatly reduced. This suggests a very high rate of exchange between Mindanao and these 2 nearby islands on the eastern routes. The slightly higher indices between Mindanao and Bohol as compared to those between Mindanao and Leyte may be partly the result of lesser knowledge of the fauna of Leyte. However, it may also be the result of some exchange across a direct Mindanao-Bohol route.

The relatively high Mindoro-Negros index for each taxon, as well as for the total herpetofauna, may be in part due to their positions at the distal end of dispersal routes, and, consequently, the same species have tended to reach both. However, it also suggests an active Mindoro-Panay-Negros dispersal route. The richer fauna of Negros, on the other hand, also indicates that a part of the Negros fauna must have arrived by way of the shorter Mindanao-Leyte-Bohol, or Mindanao-Leyte-Cebu dispersal routes, or in some instances perhaps, a Mindanao-Bohol-Negros route.

The progressively lower indices with Mindanao, as one progresses along the eastern dispersal route to Mindoro, appears to be consistent with the decrease in diversity. The Mindoro-Mindanao index is higher for frogs than for either lizards or snakes. This would be expected in terms of a later arrival, which might be accounted for by their slower dispersal ability where marine barriers have presumably operated.

Evidence for Over-Water Dispersal

In addition to the evidence of barriers to dispersal indicated by the reduction of numbers of species on distal islands as compared to proximal islands, when the size variable is minimized, as suggested in the section on diversity (fig. 2), the data may be further analyzed in terms of the probable differential effect of marine barriers. As noted at the close of the previous section, on biological grounds marine barriers would be expected to affect adversely dispersal of amphibians to a greater extent than that of reptiles. Therefore, on the assumption that the primary entryway into the Philippine archipelago was from Borneo by way of Mindanao, the amphibia might be expected to exhibit a more rapid reduction in number of species than do the reptiles when comparisons are made between Mindanao and the more distal islands such as Bohol, Negros, Mindoro, and Luzon if dispersal did take place wholly or in part across such barriers along these eastern routes. This should become even more evident if, as well as the nonnative, the presumably older endemic relict elements, those which exhibit the typical relict pattern of chance pockets of isolated species and or secondary radiation centers on distal islands, were also excluded.

To evaluate this, we propose a simple proportional-diversity index. This makes possible an objective comparison of changes in diversity for amphibia relative to changes in diversity for the reptiles. The index is calculated as the ratio of the number of species in the particular taxon (frogs, lizards, etc.) to the number of species in the total herpetofauna.

This index for frogs is indeed lower for Luzon, Negros, and Mindoro, at the distal end, than for Mindanao or Bohol at the proximal end of the dispersal routes. The amphibian index for Bohol is noteworthy in that it is slightly higher than that for Mindanao. This may be, at least in part, a distortion due to a disproportionately poorly known snake fauna (see p. 119).

Since indices for reptiles (both lizards and snakes) tend to increase as the index for amphibians decreases, it is interesting to note that the index for lizards exhibits a greater increase than that for snakes in all instances, except for Luzon Island, when the distal islands are compared with Mindanao at the entryway. For some reason, snakes appear to have been relatively more successful in their dispersal to Luzon, or have suffered fewer extinctions there.

We interpret these changes in the proportional diversity indices as supporting the conclusion that much of the herpetofauna of the Philippines, with the exception of that of Palawan, has been the result of waif dispersal across marine

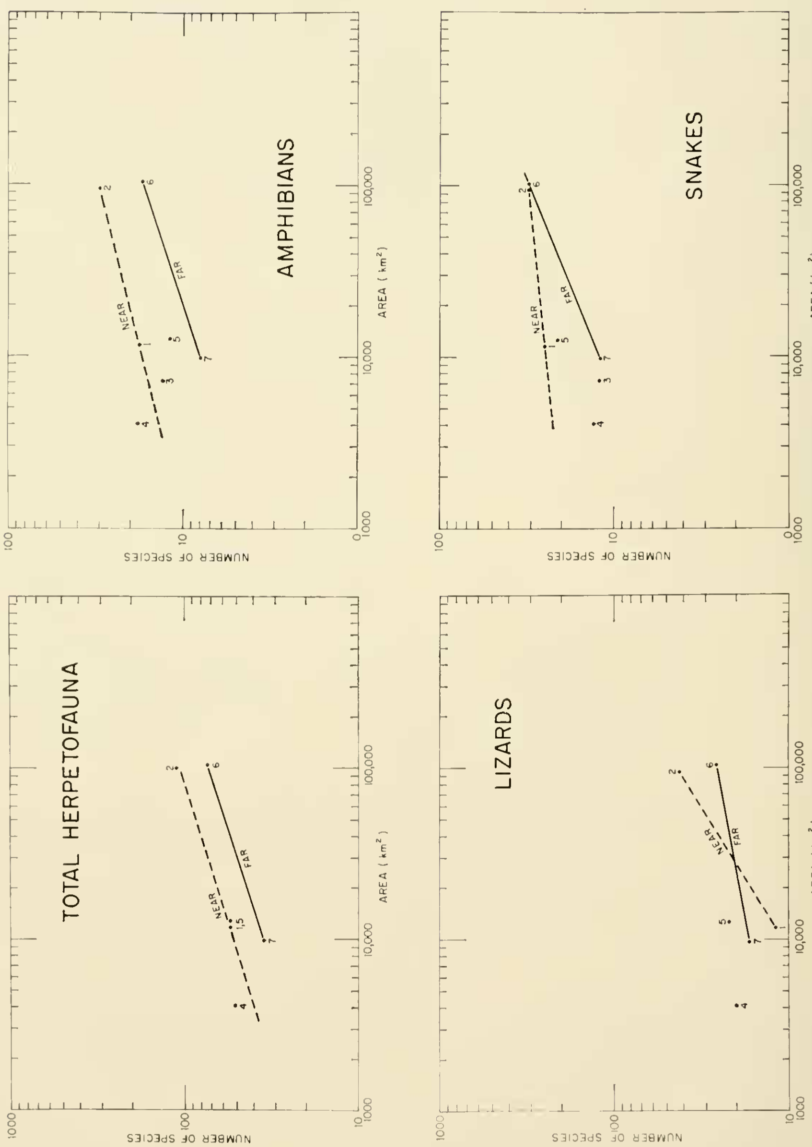

Figure 6. Area-species curves for near and far islands: (1) Palawan; (2) Mindanao; (3) Leyte; (4) Bohol; (5) Negros; (6) Luzon; (7) Mindoro.

Table 10. *Proportional diversity indices for caecilians, frogs, lizards, and snakes for selected proximal, intermediate, and distal islands for the total herpetofauna, the fauna with the presumed nonnative species excluded (in parentheses), and with both the nonnative and that element classified as relict included [in brackets].*

	Palawan	*Mindanao*	*Bohol*	*Negros*	*Mindoro*	*Luzon*
Number of Caecilian species	0.013	0.008				
(Total herpetofaunal species)	(0.018)	(0.009)				
	[0.019]	[0.011]				
Number of frog species	0.269	0.272	0.292	0.205	0.207	0.223
(Total herpetofaunal species)	(0.309)	(0.291)	(0.352)	(0.218)	(0.216)	(0.230)
	[0.302]	[0.292]	[0.333]	[0.178]	[0.188]	[0.186]
Number of lizard species	0.295	0.416	0.431	0.423	0.466	0.362
(Total herpetofaunal species)	(0.218)	(0.408)	(0.392)	(0.400)	(0.459)	(0.351)
	[0.208]	[0.391]	[0.381]	[0.400]	[0.469]	[0.322]
Number of snake species	0.423	0.312	0.278	0.372	0.328	0.415
(Total herpetofaunal species)	(0.455)	(0.301)	(0.255)	(0.382)	(0.324)	(0.419)
	[0.422]	[0.315]	[0.286]	[0.422]	[0.344]	[0.492]

barriers from Mindanao Island. This conclusion is most strongly evidenced when nonnative and isolated relict species are excluded leaving the so-called immigrant species (table 10).

Diversity as Related to Area and Distance

Area. When number of native species is plotted against area (fig. 6) for the compact group of islands included in the present study, the curves for amphibians and the total herpetofauna exhibit the expected pattern for overwater dispersal as postulated by MacArthur and Wilson (1963, 1967). Large islands do exhibit a greater diversity (number of species) than small islands and near islands a consistently greater diversity than more distant islands, in terms of the probable migration routes.

The diversity of lizards on Palawan, a near small island, and the diversity of snakes of Mindanao are somewhat less than expected, however, based on the slope of the curves. The diversity of snakes on Luzon, the most distant large island, also appears slightly greater than might be expected. One explanation might be that the relatively short over-water distances obtaining in this compact archipelago have made possible a higher frequency of invasion of snakes along the eastern chain to Luzon or that there are more relict snakes on Luzon. Since lizards of the endemic genus *Brachymeles* are absent from Palawan, this probably accounts in part for the lower diversity of this faunal group on that island. The diversity for amphibians and lizards on Bohol Island is greater than expected and that of the snakes lower. It has been suggested that the latter may be due

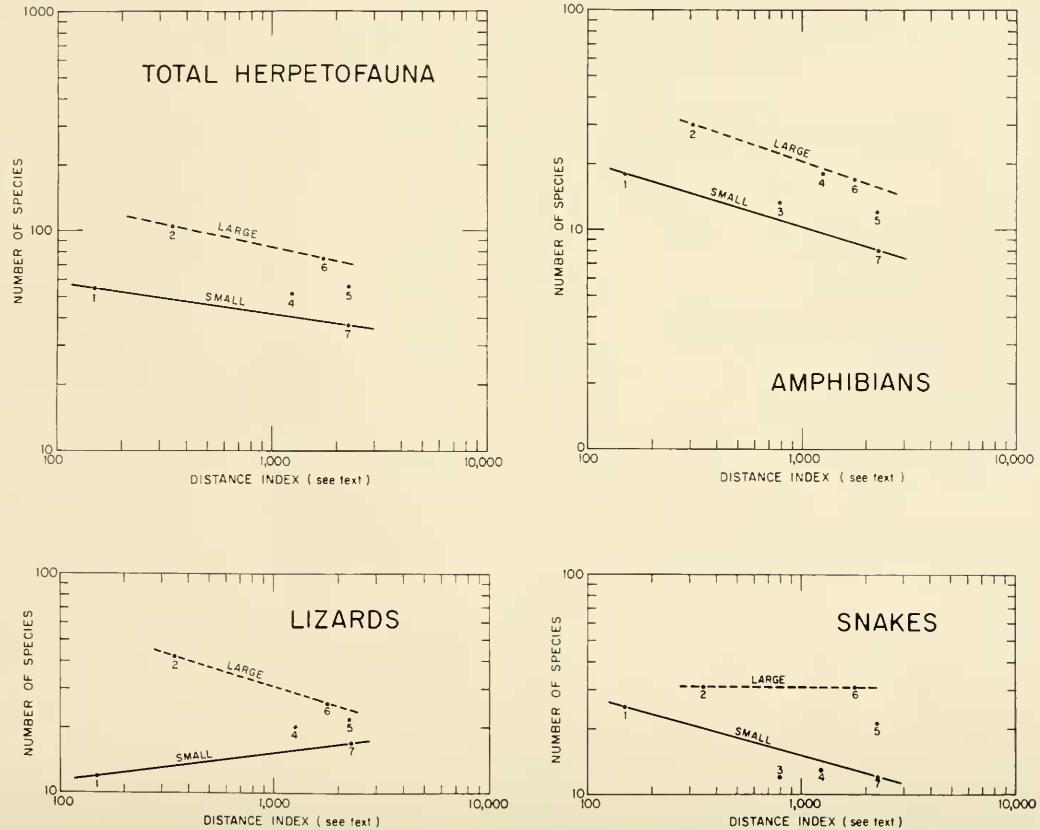

Figure 7. Distance index-species curves for large and small islands: (1) Palawan; (2) Mindanao; (3) Leyte; (4) Bohol; (5) Negros; (6) Luzon; (7) Mindoro.

TABLE 11. *Calculated distance index for Philippine islands included in this study in relation to Borneo.*

Route	*Weighted number of effective marine barriers*	*Approximate over-water distance by present probable routes (in km.)*	*Weighted distance index*
Borneo—Palawan	(1)	150	150
Borneo—Sulus—Mindanao	(1)	345	345
Borneo—Mindanao—Leyte	(2)	395	790
Borneo—Mindanao—Leyte—Bohol	(3)	420	1260
Borneo—Mindanao—Leyte—Cebu —Negros	(4–5=4½)	505	2272.5
Borneo—Mindanao—Leyte—Samar —Luzon	(4)	440	1760
Borneo—Mindanao—Leyte—Samar —Luzon—Mindoro	(5)	455	2275

to a sampling bias. The high diversity of lizards and amphibians may possibly be the result of the very narrow water gap between Leyte and Bohol.

Distance. Any attempt to measure over-water dispersal distances in this compact, nonlinear archipelago is difficult. If the effective distance is measured as the airline distance from Borneo to the various islands, Leyte is almost as distant as Luzon, and Bohol almost as distant as Mindoro (fig. 1b). If the effective distance is measured as the sum of the breadth of over-water distances between islands, by ways of eastern migration routes for all islands except Palawan, assuming that the islands themselves provide stepping stones of ecologically relatively uniform space, the effective over-water distance between Mindanao and Luzon, the northernmost island, is 75 kilometers as compared to 55 to 90 kilometers as the effective over-water distance between Mindanao and Bohol for example. In an attempt to minimize these sources of error we have derived a weighted index by multiplying the sum of the approximate over-water distances times a value for number of marine barriers (table 11).

When this distance index is plotted against number of species (fig. 7), the shape of the curves are again, with slope opposite to that of the area curves, in keeping with that expected for amphibians and the herpetofauna as a whole, and the curves for large and small islands are nearly parallel. The diversities for snakes on Mindanao and Luzon and for lizards on Palawan also impose effects on the slopes of the curves which are comparable to the effects on the area curves. Bohol and Leyte also exhibit a very low diversity for snakes relative to the curve for other islands in the same general size-category. The general agreement between these curves and those based on area suggests that such a weighted distance index may be useful in the island faunas in similar compact archipelagos.

SUMMARY AND CONCLUSIONS

The existence of relict patterns and secondary radiation centers, the relative importance of possible internal migration routes from alternative entryways, the evidence for over-water dispersal of the "migrant" element, and the effects of island area and distance are considered for the herpetofauna of the Philippines, a compact, fringing archipelago. Evaluations are based primarily on diversities and relationships of the herpetofaunas of 7 of the islands, which have a total of 220 species (54 amphibians, 92 lizards, and 74 snakes). Only in the evaluation of relict distributions is the known herpetofauna of the total archipelago taken into consideration.

The distributional patterns within the Philippines of the endemic, multi-species genera of lizards, *Luperosaurus* and *Brachymeles,* as well as the amphibian genus *Platymantis,* exhibit relict patterns of the type resulting from partial extinction of an old fauna, which has existed as a number of isolated units. *Brachymeles* and *Platymantis* also give evidence of secondary radiation centers in distal islands. Patterns for the endemic genus of lizards *Pseudogekko* and snake genera *Cyclocorus, Hologerrhum,* and *Oxyrhabdium* are simpler relict patterns with only 1 or 2 species in each genus. These are rather widely distributed, or, in some instances, limited to either the distal or proximal islands. These patterns are those postulated by Darlington (1957) as patterns which would develop within a chain of islands.

Sorenson's index of similarity is used to evaluate the relative effectiveness of dispersal routes. These indices, particularly when the nonnative fauna is excluded, indicate that the primary dispersal route or routes within the archipelago have been the eastern routes, by way of the Mindanao-Leyte—or possibly, in some instances the Mindanao-Bohol—pathways. The Palawan entryway has contributed very little to the herpetofauna of the rest of the Philippines. High indices of similarity between Negros and Mindoro suggest a relatively active migration route between these two islands.

A proportional-diversity index, based on the presumed lower ability of amphibians to disperse across marine barriers, is used to evaluate the probable effect of marine barriers. The evidence indicates that, with the exception of Palawan Island, much of the herpetofauna has apparently reached the intermediate and distal islands of the archipelago from Mindanao as a result of waif dispersal across marine barriers.

When number of species for the total herpetofauna, and for the amphibians, lizards, and snakes independently, are plotted against area or against a weighted distance value the curves for amphibia and the total herpetofauna exhibit patterns consistent with those projected from MacArthur's and Wilson's thesis (1967) regarding faunal diversity along a chain of islands of varying size. The data indicate, however, that the diversity of the lizard fauna on Palawan island is lower than expected, and that the diversity of the snake fauna is probably somewhat lower for Mindanao and higher for Luzon island relative to the diversity exhibited by the fauna of other islands in the study. The effects of the narrow marine barriers on the present distribution of the amphibian fauna have produced a pattern of island diversities in general agreement with the MacArthur-Wilson hypothesis. The diversities of lizards and snakes for the sample group of islands included in this study exhibit several discrepancies. The relatively narrow over-water barriers between the islands of this compact archipelago, less effectual against reptiles than amphibians, and the several possible migration routes and secondary centers of radiation may be factors in the distribution patterns of these faunal elements. The reasons, however, for the low diversity of lizards of Palawan and for the effectiveness of the barrier between Palawan and Mindoro, a marine channel only about 150 km. in breadth at the present time and broken by small islands, are not readily explained from data.

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